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Comparative post-fire water relations of selected reseeding and resprouting fynbos plants in the Jonkershoek Valley, Cape Province, South Africa

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Leaf area development has been proposed as a simple predictor of post-fire streamflow response in the mountain catchments of the south-western Cape, South Africa. Implicit in this proposal is the assumption that transpiration rates per unit leaf area of reseeders and resprouters are similar. This assumption was tested by studying the water relations of selected fynbos plants after a fire in a mountain catchment in the Jonkershoek Valley near Stellenbosch for nearly two years. Stomatal conductances and xylem pressure potentials were measured and transpiration rates were estimated for three reseeding species and four resprouting species. There was no clear difference between the daily transpiration rates of reseeding and resprouting plants. The shallow-rooted resprouters responded similarly to the reseeders; moderate water stress (–3 to –4 MPa) and reduced transpiration (< 1 mmol m^{-2} s^{-1}) were experienced during the first two summers after fire. The deep-rooted resprouters did not show water stress during summer, and transpiration rates were moderate throughout the year. Annual patterns of water use per unit leaf area were similar for reseeders and resprouters. Leaf area may therefore be used as a simple predictor of post-fire streamflow response.

Daar is voorgestel dat blaaroppervlakontwikkeling as 'n eenvoudige voorspeller van na-brandse stroomvloei-reaksie in die bergopvanggebiede van die Suidwes-Kaap, Suid-Afrika, kan dien. Hierdie voorstel impliseer dat die transpirasie-tempo per eenheid oppervlakte van saaiers en uitspruiters soortgelyk is. Hierdie veronderstelling is getoets deur die waterverhouding van sekere fynbos plante te bestudeer vir 'n tydperk van amper twee jaar na 'n brand in 'n bergopvanggebied in die Jonkershoekvallei naby Stellenbosch. Blaarkonduktansie en xileemdrukpotensiaal is gemeet en die tranpirasie-tempo van drie saaierplantsoorte en vier uitspruiter-plantsoorte is beraam. Daar was geen noemenswaardige verskil tussen die daaglikse transpirasie-tempo's van saaiers en uitspruiters nie. Die uitspruiters met vlak wortelstelsels en die saaiers het 'n soortgelyke reaksie getoon; in albei gevalle is matige waterspanning waargeneem (–3 tot –4 Mpa) en het verminderde transpirasie plaasgevind (< 1 mmol m^{-2} s^{-1}) gedurende die eerste twee somers na die brand. By die diepgewortelde spruiters is waterspanning nie gedurende die somer waargeneem nie en transpirasie-tempo's was matig dwarsdeur die jaar. Die jaarlikse patroon van waterverbruik per eenheid blaaroppervlakte was soortgelyk vir saaiers en uitspruiters. Blaaroppervlakte kan dus gebruik word as 'n eenvoudige voorspeller van na-brandse stroomvloei reaksie.

Keywords: Fynbos, mediterranean-type ecosystems, reseeders, resprouters, water relations

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Introduction

Changes in water yield from mountain fynbos catchments are directly related to changes in plant biomass (Wicht 1971). Burning, which is carried out to reduce fire hazard, to control invasive plants and to rejuvenate the fire-adapted fynbos vegetation, reduces plant biomass and therefore has a marked influence on catchment water yield (Bosch *et al.* 1984). Results from experimental burns in fynbos are inconsistent, but show that fires usually produce short-lived increases in catchment water yield (Bosch *et al.* 1984; Lindley 1986; Lindley *et al.* 1988). Bosch *et al.* (1986) have argued that the duration of the increased streamflow depends on the type of vegetation, its condition (pristine or degraded), and on the canopy recovery rate. The recovery rate depends on the pre-fire composition of the fynbos community, especially the ratio of reseeding to resprouting plants (hereafter termed reseeders and resprouters). The relative abundance of these life forms is influenced by fire frequency; short fire cycles favour resprouters (especially graminoids), longer fire cycles favour reseeders (van Wilgen 1982; Kruger & Bigalke 1984). Frequent burning reduces biomass by eliminating most obligate reseeding shrubs (van Wilgen & Kruger 1981) which usually make up the greatest part of the biomass (van Wilgen *et al.* 1985). Resprouters are more resilient to increased frequency of fire (Keeley 1986). It is therefore possible to manipulate the relative abundance of reseeders and resprouters in a fynbos catchment by manipulating the fire regime.

Leaf area development (or biomass recovery) in communities dominated by obligate reseeders is slower after a fire than in communities dominated by resprouters. This led Bosch *et al.* (1986) to suggest that the gradient of water yield reduction will be less steep in communities dominated by reseeders. Little is known, however, of the water relations of plants after fires in fynbos ecosystems. Resprouters, with their rapid post-fire canopy development, regain their prefire biomass soon after fire. Reseeders take longer to develop their canopies but their biomass may eventually equal or exceed that of resprouters. Resprouters should therefore use more water than reseeders in the early post-fire period, simply by virtue

of their greater leaf area. Inherent in this hypothesis is the assumption that transpiration rates per unit leaf area of reseeders and resprouters are similar.

In this paper, we test the assumption that reseeders and resprouters have similar transpiration rates and therefore that leaf area alone can be used as a simple predictor of post-fire changes in water yield. We determined stomatal conductances, leaf xylem pressure potentials and transpiration rates, and examined the relationships between environmental- and plant-response factors for the selected species.

Study site and species

The study was conducted in Swartboskloof in the Jonkershoek Valley (33°57'S 18°55'E) near Stellenbosch, in the Cape Province of South Africa. The area has a mediterranean climate with warm, dry summers and cool, wet winters. The mean maximum and minimum temperatures for the hottest month of the year (February) are 27.3 and 14.5°C respectively and those for the coldest month (July) are 16.8 and 6.2°C respectively. Mean annual rainfall is 1 475 mm, of which approximately 67% falls between May and September (Richardson & Fraser in press).

The soil is derived from granite and quartzite and its form is classified as Oakleaf (Series 31/34) (MacVicar *et al.* 1977). It is moderately drained with a varying percentage of stones and boulders in the profile (Fry 1987), being as shallow as 400 mm in places. The slope of the site is approximately 4° with a north-facing aspect, and the altitude is 305 m.

The dominant vegetation type on the study site is Jonkershoek Mesic Proteoid Fynbos, which comprises a tall (2–3 m) open to closed proteoid overstorey with a mid-high (*ca.* 1 m) understorey (Campbell 1985; Mc Donald 1985). The Swartboskloof vegetation was 29 years old at the time of a prescribed burn in 1987. The species chosen for this study are representative of the major plant forms in the fynbos vegetation of Swartboskloof (Table 1). They were sampled in close proximity of each other (5–10 m radius), on similar soils with the same aspect.

Table 1 Family, growth form, regeneration mode and root characteristics of study species

Species	Family	Growth form	Mode of regeneration	Root type*
Protea repens	Proteaceae	Tall shrub	reseeder	2
Protea nitida	Proteaceae	Tall shrub	reseeder/ sprouter	1/2**
Leucadendron salignum	Proteaceae	Low shrub	resprouter	2
Cliffortia cuneata	Rosaceae	Mid-high shrub	reseeder	2
Watsonia borbonica (syn. *W. pyramidata*)	Iridaceae	Geophyte	resprouter	3
Ischyrolepis gaudichaudianus	Restionaceae	Graminoid/ Aphyllous	resprouter	4

*after Higgins *et al.*1987:

1: short, shallow primary root, laterally extensive

2: deep tap root with lateral roots concentrated in upper soil

3: lateral roots of similar diameter originating from nodes on corm

4: shallow roots from subterranean stems, rhizomes or stolons

**reseeders have type 2 roots and resprouters type 1

Methods

Soil water potentials were monitored with porous cup Jet Fill tensiometers (Model 2724, Soil Moisture Equipment Corp., California) on the site at three depths (300, 450 and 600 mm). The presence of a shallow rock bed prevented insertion of tensiometers to greater depths. These tensiometers are limited to soil water potentials greater than –80 kPa. Soil moisture contents were measured gravimetrically during each field run. Three samples from two depths were taken per field day (upper 200 mm, and from 200 mm down to the bed rock usually 200–400 mm deep), using a soil orger.

Diurnal courses of relative humidity, air temperature, solar radiation and wind speed were available from two nearby weather stations, both approximately 500 m from the study site. Mean hourly values for each field day were calculated from readings made at 1-min intervals. Daily rainfall was also recorded.

A Scholander pressure chamber (Scholander *et al.* 1965) was used to determine xylem pressure potentials on three leaves per species (one per plant irrespective of growth form). Mature leaves (except for the juvenile reseeders) were selected from the same position on each of the shrubs (both reseeders and resprouters) for consecutive measurements. Additional leaves were measured when variation within species exceeded 0.15 MPa. Measurements commenced before dawn (between 04:00 and 06:00 depending on the season) and were repeated at 2-h intervals throughout the day until dusk.

Diurnal courses of stomatal conductance were determined at monthly intervals between September 1988 to November 1989, with a null-balance diffusion porometer (model MCS 301 M C Systems, Plumstead, South Africa) (Beardsell *et al.* 1972). A single mature leaf (or shoot if the leaves were very small), was selected on five separate plants of each species (irrespective of regeneration mode). The leaves were selected from the same height and aspect in the canopy. The reseeders were 18 months old at the start of the study. This was also the age of the above-ground biomass of the resprouters. Measurements were repeated on these five leaves throughout the day at hourly intervals from daybreak until dusk. The days on which measurements were taken were standardized as far as possible with regards to weather; clear still days were preferable. The leaf areas of the sample leaves were determined at the end of a day's measurements. Estimates of total transpiration per unit leaf area per day were obtained by determining the area under the diurnal hourly transpiration rate curves for each species.

A stepwise regression analysis (PROC STEPWISE in SAS; SAS inc. 1985) was carried out to determine the proportion of the variation in transpiration rate explained by the following variables: mean hourly solar radiation temperature and vapour pressure deficits, and daily soil moisture content.

Correspondence analysis was employed on a matrix of predawn and midday xylem pressure potentials, mean and peak daily stomatal conductances and transpiration rates, and total daily water use per unit leaf area, to compare the

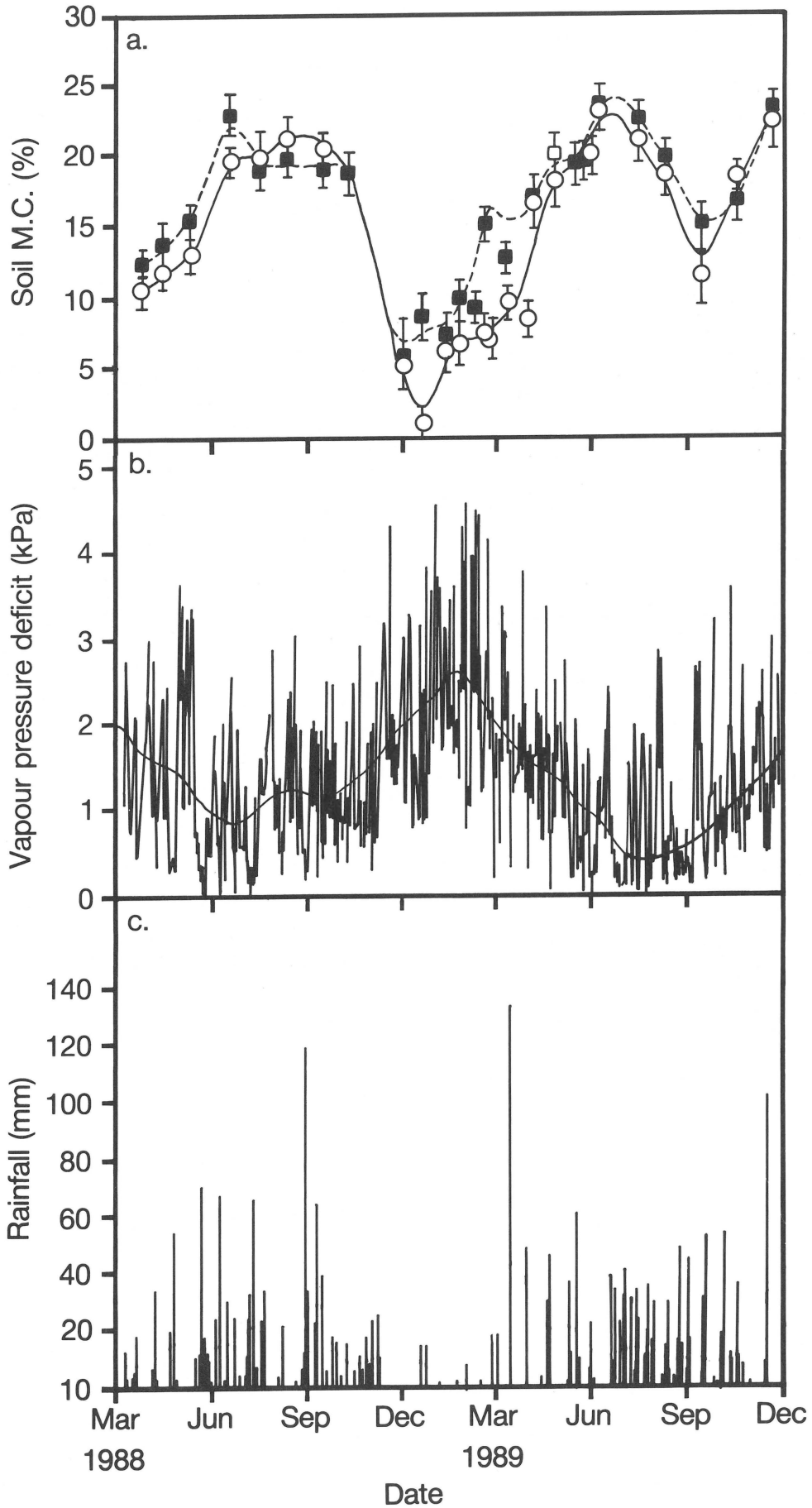

Figure 1 Seasonal fluctuations in (a) soil water content (circles = upper 200 mm; squares = 200–400 mm; (b) maximum daily vapour pressure deficit [the smoothed line fitted by spline interpolation (I = SM35 in SAS inc. 1985) indicates the seasonal trend] ;(c) daily rainfall for the period March 1988 to November 1989.

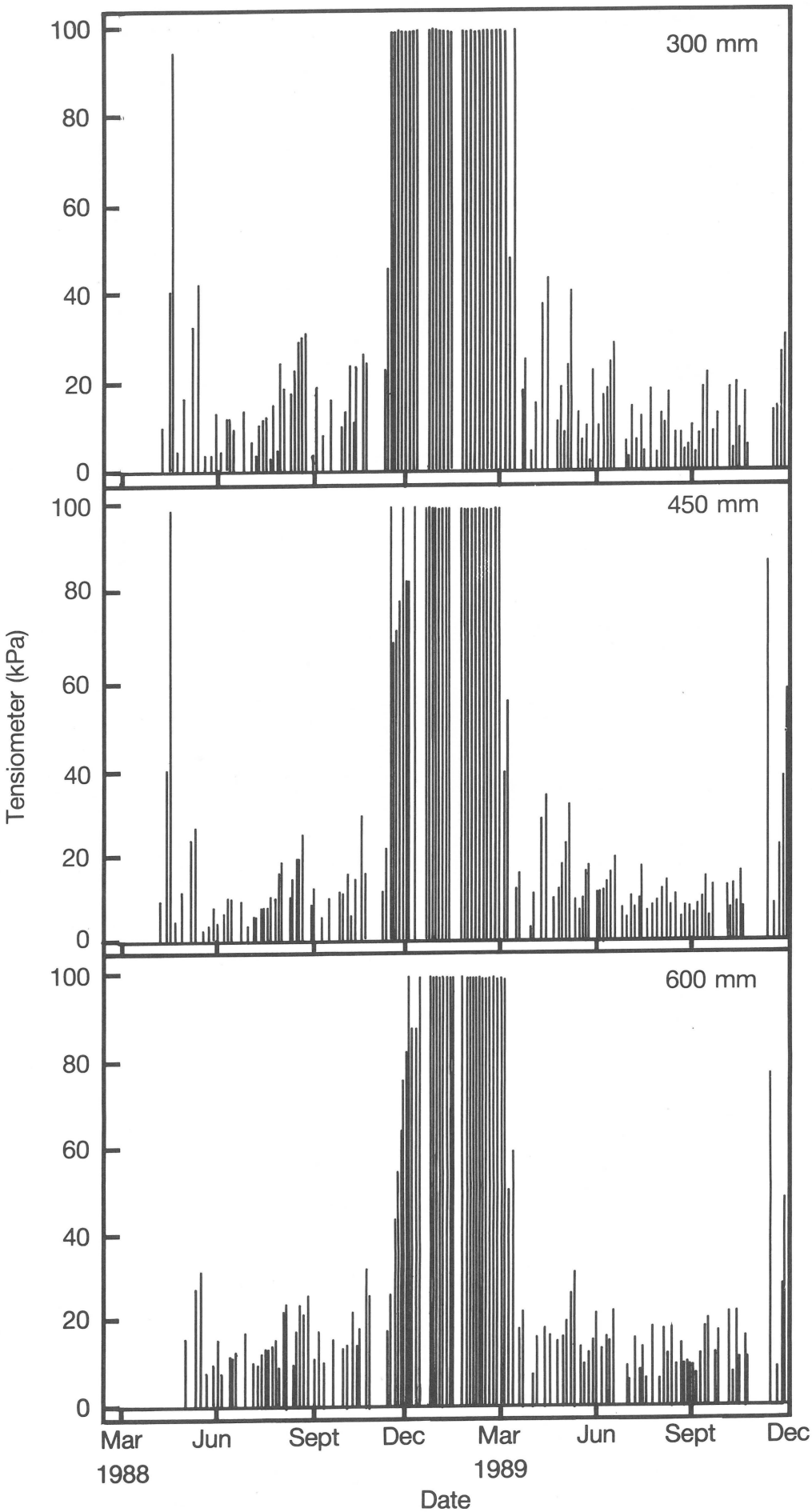

Figure 2 Seasonal variation in the soil water potential at the study site, measured at the following depths: (a) 300 mm, (b) 450 mm and (c) 600 mm.

response of the different species and regeneration types to environmental conditions in the early post-fire phase. Each row in the matrix summarized the physiological response of a species or regeneration type on one day. This matrix was standardized to prevent distortion by the different scales of the variables, giving each variable equal weight, and then ordinated using the correspondence analysis algorithms described by Underhill & Peisach (1985).

Results

Gravimetric soil water content ranged from *ca.* 2% in summer to *ca.* 22% in winter in the upper *ca.* 400 mm of the soil surface (Figure 1a). All three sets of tensiometers showed the same pattern of soil water potential throughout the year. Potentials ranged between –5 and –40 kPa throughout the year (Figure 2) with the exception of December to March (summer to early Autumn) when water potentials exceeded the range of the tensiometers (< –80 kPa). Vapour pressure deficits were highest during the dry summer period and lowest during the wet winter months (Figure 1b). The soil water potentials and water contents mirrored the rainfall pattern (Figure 1c).

Predawn xylem pressure potentials remained above –1.2 MPa for all species except during January 1989 and February 1988 and 1989, when the reseeders (all shallow-rooted at 18 months) experienced moderate water stress (predawn potentials of –2.5 to –3 MPa) (Figure 3a). The resprouters were less stressed and maintained predawn water potentials above –1.5 MPa (Figure 3b), except *I. gaudichaudianus* (shallow-rooted). During most of the year, xylem pressure potentials of all the species returned to predawn levels at dusk. The dusk potentials during November and December 1988 were, however, somewhat lower than the predawn levels, reflecting the onset of moderate soil water deficits. In January and February 1989, the soil was extremely dry, especially in the upper 450–600 mm (Figures 1a & 2), and for all species, dusk potentials were lower (more negative) than predawn potentials. Most of the deeper-rooted resprouters managed to take up sufficient water to return their potentials to values near their predawn levels, but the shallow-rooted reseeders and *I. gaudichaudianus* remained at levels similar to those at midday.

Midday potentials were also much lower (more negative) in summer for the reseeders than for the resprouters, with the exception of shallow-rooted *I. gaudichaudianus*) (Figure 3c & d). *Watsonia borbonica* and *P. nitida* resprouts showed no signs of diurnal or seasonal water stress and their potentials remained above –2 MPa.

Conductances for all species were low during the dry summer months of November to March, usually remaining below 100 mmol m^{-2} s^{-1} throughout the day. The reseeders displayed low peak conductances (< 100 mmol m^{-2} s^{-1}) at their lowest predawn potentials (–3 to –4 MPa) in summer. Peak conductances of 200 to 500 mmol m^{-2} s^{-1} were maintained during the rest of the season (Figure 4). *Protea nitida* and *L. salignum* (resprouters) maintained peak conductances of *ca.* 100 to 200 mmol m^{-2} s^{-1} under their lowest predawn potentials (–0.5 to –0.7 MPa). Peak conductances during the rest of the season ranged from *ca.* 100 to 450 mmol. *Watsonia borbonica* exhibited high conductances (maximum rates of 300 to 600 mmol m^{-2} s^{-1}) throughout its annual cycle (Figure 4). *Watsonia borbonica* is deciduous and loses its leaves at the start of the dry period (November). The first new shoots appear in February at the end of summer (P.J. Brown pers. comm.). *Ischyrolepis gaudichaudianus*

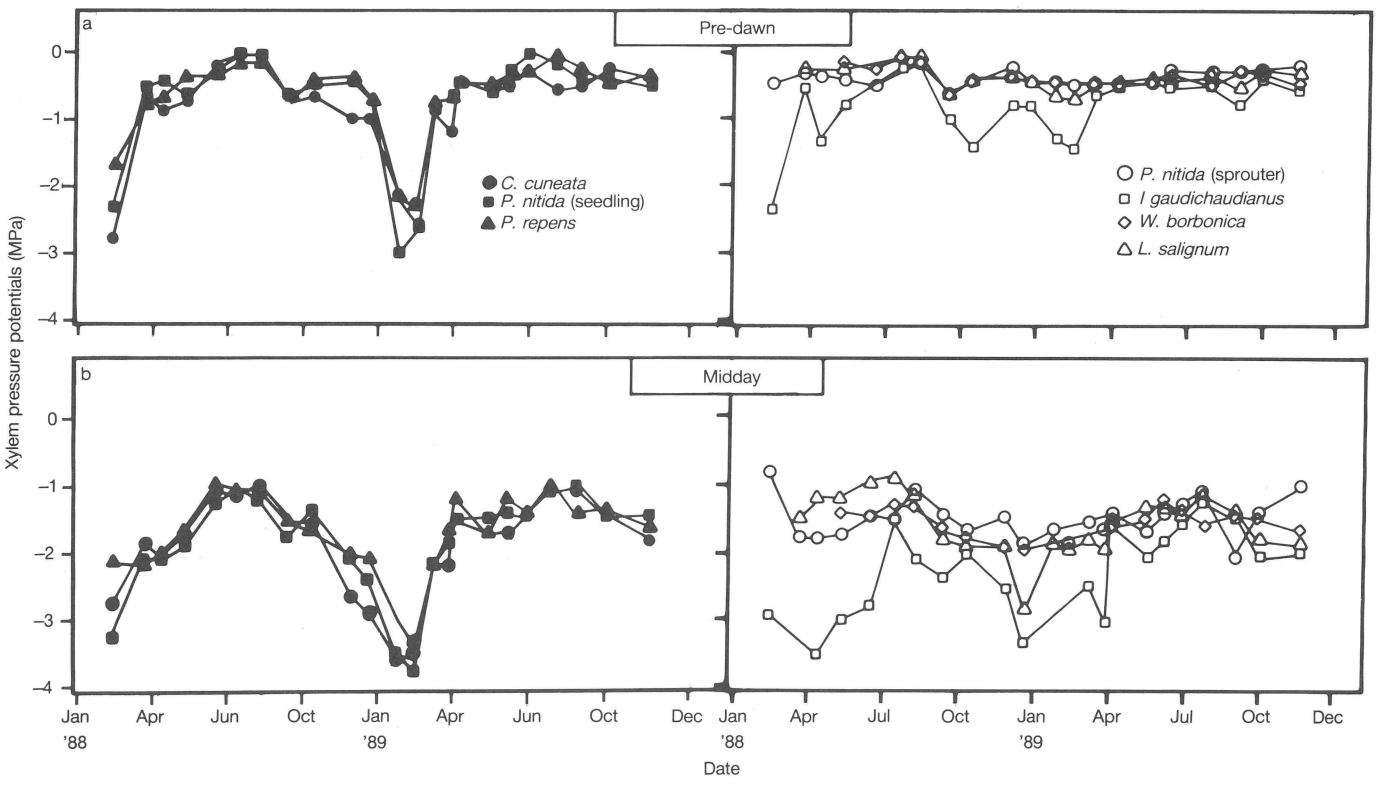

Figure 3 The predawn (a) and midday (b) xylem pressure potentials for the reseeders (solid symbols) and resprouters (open symbols).

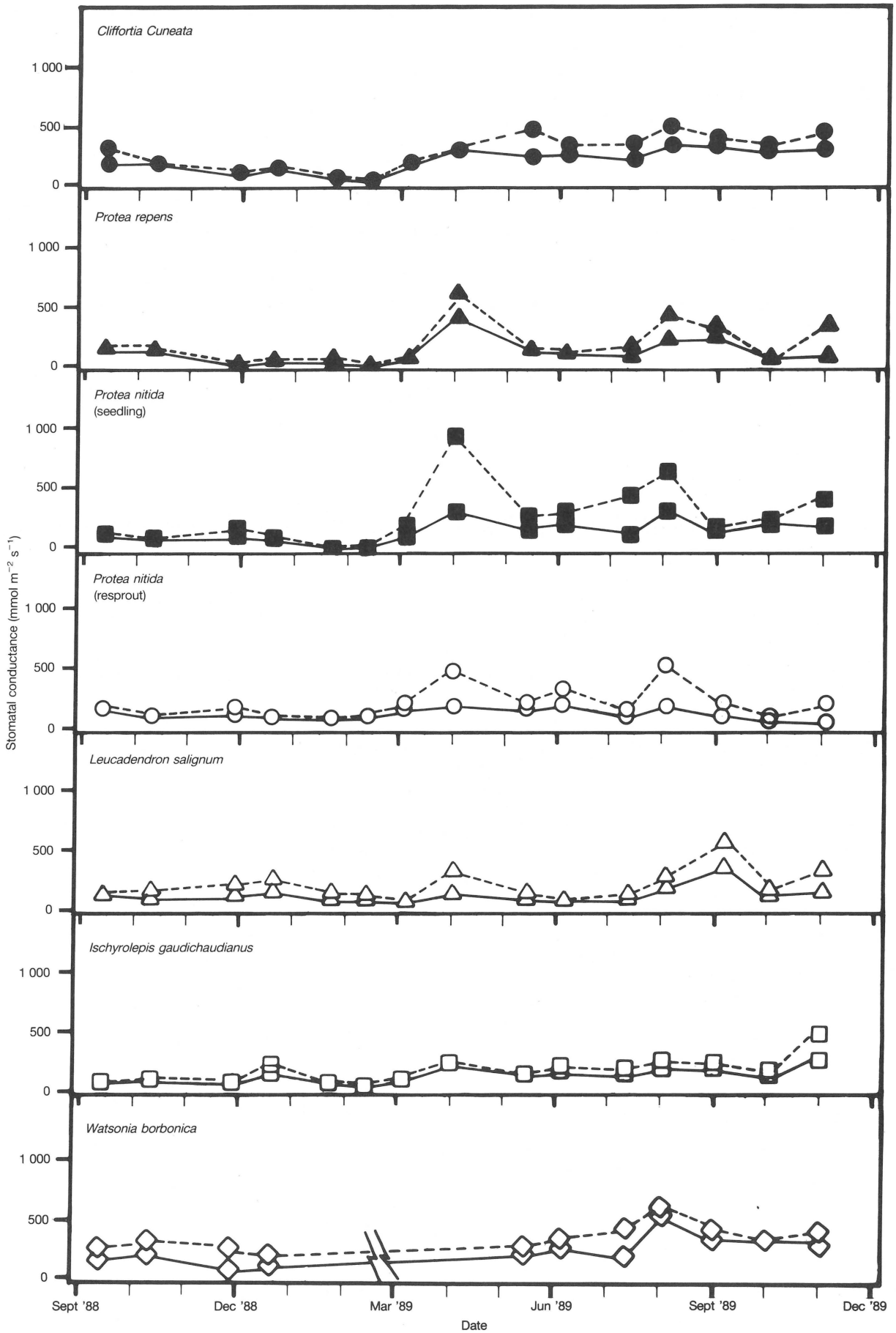

Figure 4 The median (solid line) and peak (stippled line) stomatal conductances for each measurement day (September 1988 – December 1989). The solid symbols represent the reseeders and the open symbols represent the resprouters.

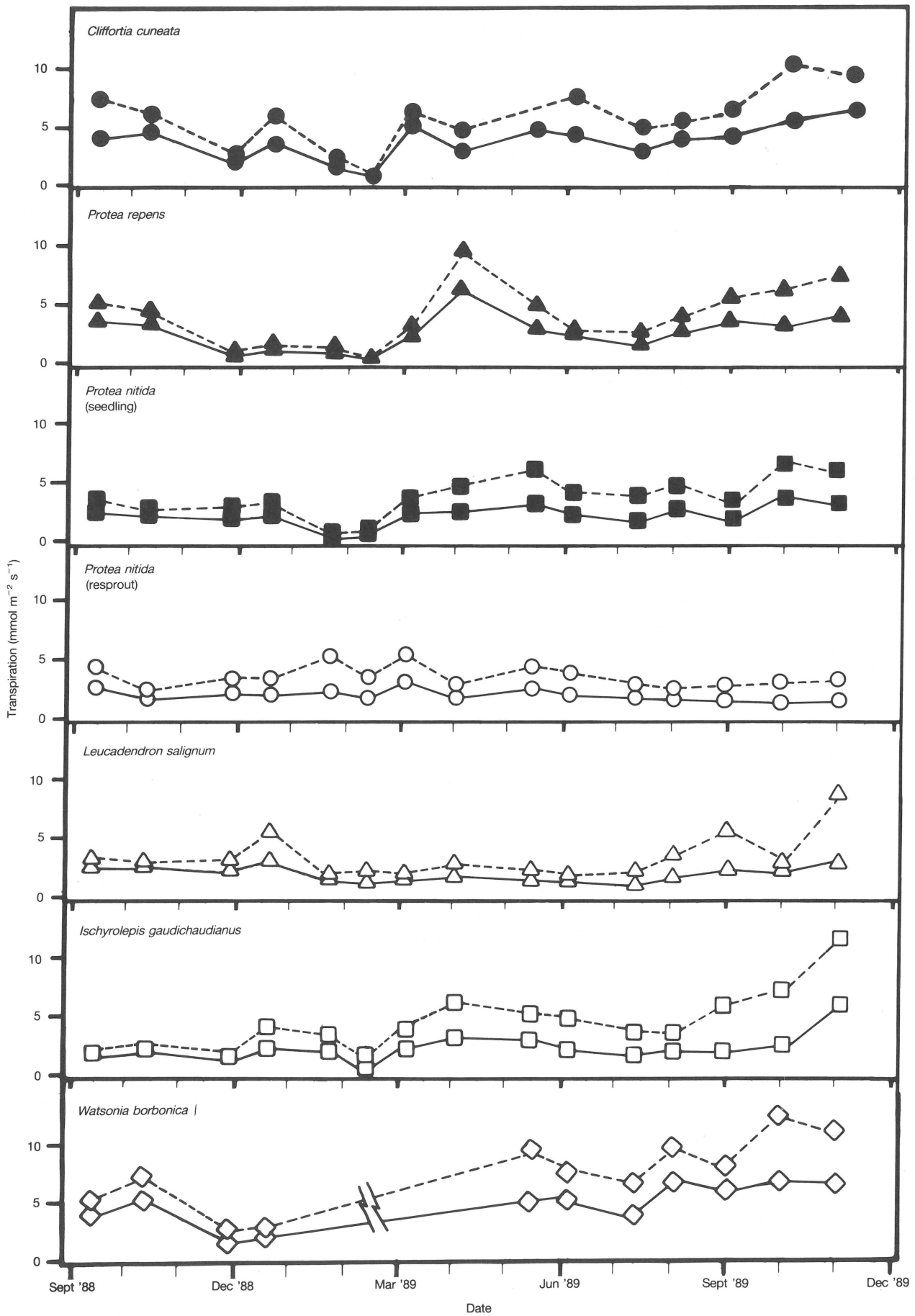

Figure 5 The median (solid line) and peak (stippled line) transpiration rates for each measurement day (September 1988 – December 1989). The solid symbols represent the reseeders and the open symbols represent the resprouters.

showed a slight decline in stomatal conductance from a maximum rate of *ca.* 250 mmol m^{-2} s^{-1} in winter to *ca.* 150 mmol m^{-2} s^{-1} in summer (Figure 4). All plants showed an increase in stomatal conductance immediately after the first winter rains at the end of March, probably due to the replenishment of soil water supplies after the summer drought (250 mm of rain fell between the March and April 1989 measurements). The effect was more marked for the reseeders than the resprouters (e.g. *P. nitida* seedlings and resprouts in Figure 4). There were no clear differences in mean and peak stomatal conductance between species for most of the year (excluding summer).

Transpiration rates were highest for most species during April and May 1989 after the first heavy rains fell in March. Mean daily peak transpiration rates were low during the summer drought in February 1989 (*ca.* 1 mmol m^{-2} s^{-1}). During summer, resprouters of *P. nitida* and *L. salignum* maintained higher mean transpiration rates than any of the reseeders (between 2 and 4 mmol m^{-2} s^{-1}) (Figure 5). Rates also declined later in the season. There was a slight lag effect however, as transpiration rates are not solely affected by stomatal conductance but are also driven by leaf-to-air vapour pressure deficits. *Watsonia borbonica* maintained a high transpiration rate throughout the season, with its peak daily rates ranging from 5 to 8 mmol m^{-2} s^{-1}. The mean hourly rate for this species ranged from 2 to 5 mmol m^{-2} s^{-1} (Figure 5). *Ischyrolepis gaudichaudianus* showed a slight decline in transpiration rate from winter to summer as the predawn xylem pressure potentials dropped, but still maintained relatively high transpiration rates (peak rates of 2 to 4 mmol m^{-2} s^{-1}) under increasing stress. Peak and mean transpiration rates were, with the exception of the summer drought period, generally higher for the shallow-rooted species than the deeper-rooted species.

In general, the variables temperature, vapour pressure deficit (VPD), solar radiation and soil water content explained most of the variation in transpiration rates for all species (Table 2). Patterns were, however, not entirely consistent for any groups of species. The only conclusions that could be made from the regression analysis was that VPD and soil water content were generally the most significant variables explaining the variation in reseeder transpiration rates during summer and spring. During the rest of the year, soil water content played a less significant role. The variation in resprouter transpiration rates was generally explained by changes in solar radiation and VPD during most of the year. In summer, soil water content was more important than solar radiation in determining the transpiration rate of *Leucadendron salignum*.

The ordination by correspondence analysis separated species/regeneration types along axis 1 mainly by extreme xylem pressure potentials, and along axis 2 mainly by peak conductance rates and daily water use (Figure 6a). Shallow-rooted resprouters (*I. gaudichaudianus*) and reseeders (*P. nitida, P. repens* and *C. cuneata*) showed the most negative xylem pressure potentials during summer; this group is clustered to the right of the origin on axis 1. Deep-rooted plants show little 'movement' through ordination space over seasons (Figure 6b); they are less affected by environmental fluctuations than the shallow-rooted plants. The latter

Table 2 Regression coefficients for the reseeding and resprouting shrub species for the dependent variable transpiration, calculated as the mean of the hourly replicates (*P < 0.05; **P < 0.01; ***P < 0.001)

Season	Independent variables	Partial R^2	Model R^2	Prob > F
	Leucadendron salignum (resprouter)			
Summer	Soil moisture	0.31	0.31	***
	VPD	0.21	0.52	***
	Temperature	0.07	0.59	*
	Solar radiation	0.0	0.59	
Autumn	Solar radiation	0.54	0.54	***
	Temperature	0.12	0.66	*
	Soil moisture	0.02	0.68	
	VPD	0.0	0.68	
Winter	Solar radiation	0.78	0.78	***
	VPD	0.03	0.81	
	Temperature	0.02	0.83	
	Soil moisture	0.0	0.83	
Spring	VPD	0.42	0.42	***
	Solar radiation	0.10	0.52	***
	Temperature	0.08	0.80	***
	Soil moisture	0.02	0.62	
	Protea nitida (resprouter)			
Summer	Solar radiation	0.75	0.75	***
	VPD	0.08	0.83	***
	Temperature	0.06	0.89	***
	Soil moisture	0.02	0.91	**
Autumn	VPD	0.78	0.78	***
	Solar radiation	0.04	0.82	
	Temperature	0.10	0.92	***
	Soil moisture	0.0	0.92	
Winter	Solar radiation	0.88	0.88	***
	Temperature	0.04	0.92	***
	VPD	0.01	0.93	
	Soil moisture	0.01	0.94	
Spring	VPD	0.36	0.36	***
	Solar radiation	0.07	0.43	*
	Soil moisture	0.01	0.44	
	Temperature	0.0	0.44	
	Protea nitida (seedling)			
Summer	Soil moisture	0.71	0.71	***
	Solar radiation	0.06	0.77	***
	VPD	0.0	0.77	
	Temperature	0.0	0.77	
Autumn	VPD	0.53	0.53	***
	Solar radiation	0.07	0.60	***
	Temperature	0.25	0.85	
	Soil moisture	0.01	0.86	
Winter	Solar radiation	0.52	0.52	***
	Temperature	0.13	0.65	*
	VPD	0.0	0.65	
	Soil moisture	0.01	0.66	

Table 2 Continued

Season	Independent variables	Partial R^2	Model R^2	Prob > F
Spring	Temperature	0.30	0.30	***
	Soil moisture	0.01	0.31	
	Solar radiation	0.01	0.32	
	VPD	0.01	0.33	
	Cliffortia cuneata (reseeder)			
Summer	Soil moisture	0.49	0.49	***
	VPD	0.36	0.85	***
	Temperature	0.02	0.87	
	Solar radiation	0.01	0.88	
Autumn	VPD	0.49	0.49	***
	Temperature	0.15	0.64	*
	Soil moisture	0.00	0.64	
	Solar radiation	0.04	0.68	
Winter	VPD	0.81	0.81	***
	Soil moisture	0.05	0.86	*
	Temperature	0.03	0.89	
	Solar radiation	0.01	0.90	
Spring	VPD	0.50	0.50	***
	Solar radiation	0.25	0.75	***
	Soil moisture	0.10	0.85	***
	Temperature	0.01	0.86	*
	Protea repens (reseeder)			
Summer	VPD	0.34	0.34	***
	Soil moisture	0.12	0.46	*
	Temperature	0.21	0.67	***
	Solar radiation	0.06	0.73	*
Autumn	Solar radiation	0.86	0.86	***
	Temperature	0.06	0.92	***
	VPD	0.01	0.93	
	Soil moisture	0.0	0.93	
Winter	VPD	0.74	0.74	***
	Temperature	0.12	0.86	***
	Soil moisture	0.01	0.87	
	Solar radiation	0.0	0.87	
Spring	VPD	0.38	0.38	***
	Temperature	0.32	0.70	***
	Soil moisture	0.09	0.79	***
	Solar radiation	0.0	0.79	

however show greater response to rainfall following droughts.

Discussion

Our results showed xylem pressure potentials of deep and shallow-rooted species (irrespective of regeneration mode) to be similar through most of the study period except summer. The lower potentials experienced by the shallow-rooted plants during summer appeared to be in response to low soil water potentials, the upper soil layers being drier than the lower layers (Figures 1a & 2). During summer, conductances and transpiration rates of all shallow-rooted plants decreased, probably in response to the low leaf water potentials resulting from insufficient access to soil water in the upper (drier) soil layers and a high evaporative demand (high vapour pressure deficits as in Figure 1b). The deeper-rooted resprouters probably had access to deeper, moist soil layers with relatively high soil water potentials, which enabled them to transpire at moderate rates throughout the year without experiencing lower water potentials. Conductances of these resprouters were also slightly lower in summer than in winter, possibly in response to the high vapour pressure deficits [to which conductances are usually inversely related (Larcher 1983, p.93)].

The xylem pressure potential patterns exhibited by the species in this study corresponded well with those of similar species in other fynbos studies (Miller *et al.* 1983, 1984; Miller 1985; Kruger *et al.* 1988; van der Heyden & Lewis 1988; Richardson & Kruger 1990) with the shallow-rooted reseeders and resprouters (e.g. *P. repens, I. gaudichaudianus*) responding in a similar fashion to other shallow-rooted species (e.g *Erica plukenetii*, Miller *et al.*. 1983, 1984). Deep-rooted resprouters (e.g. *L. salignum*) responded similarly to other deep-rooted species (e.g. *P. nerifolia*, Miller *et al.* 1983, 1984). In a broader context, our results are similar to those for structurally equivalent plants in other mediterranean-climate regions (e.g. shallow-rooted *Arctostaphylous* spp. and deep-rooted *Adenostoma fasciculatum*) (Poole & Miller 1975; Roberts *et al.* 1981; Dodd *et al.* 1984; Davis & Mooney 1986; Hart & Radosevich 1987). Differences in water potential between deep- and shallow-rooted plants in the chaparral were also generally small during the seasons where soil water was not limiting, but increased as soil water supplies diminished. Neither the reseeders nor resprouters in our study experienced severe drought in a mediterranean-climate context (cf. Blake-Jacobsen 1987; Roberts *et al.* 1981; Roberts 1982 where water potentials for selected chaparral shrub species in summer dropped to –7 MPa).

Daily stomatal conductance patterns could not be used to distinguish between the reseeders and resprouters of our study, or between species in general, for most of the study period. Shallow-rooted species did however have markedly lower conductances than the deeper-rooted species during the summer drought. The range of conductances of the reseeders, *I. gaudichaudianus* and the deep-rooted resprouters were similar to those of shallow- and deep-rooted plants measured both in fynbos and other mediterranean regions. All the species in our study showed decreasing conductances as the drought progressed, similar to the trends shown by *Arctostaphylous stanfordiana* and *Adenostoma fasciculatum* of the chaparral (Hart & Radosevich 1987). The shallow-rooted *A. stanfordiana*, by contrast to the shallow-rooted species in our study, displayed higher conductances than deep-rooted *A. fasciculatum* during the spring and early summer, when soil water potentials were high (Hart & Radosevich 1987). This phenomenon was also evident to some extent in the fynbos, where deep-rooted Proteaceae were found to have more moderate conductances, while shallow-rooted Ericaceae had the highest and most variable conductances (Miller *et al.* 1984). Some of the deeper-rooted fynbos species [e.g. *Elytropappus gnaphaloides* (Miller *et al.* 1983)] were

however, also shown to have high conductances.

Diurnal transpiration trends could also not be used to distinguish between reseeders and resprouters in this study, although slight differences were evident between shallow- and deep-rooted plants (with shallow-rooted plants generally having higher transpiration rates). Differences were particularly evident between shallow- and deep-rooted species during summer and after the April rains, when shallow-rooted plants had lower transpiration rates than deep-rooted plants during the drought, but higher rates during April. The shallow roots of the reseeders and *I. gaudichaudianus* enabled them to utilize rapidly surface water from the

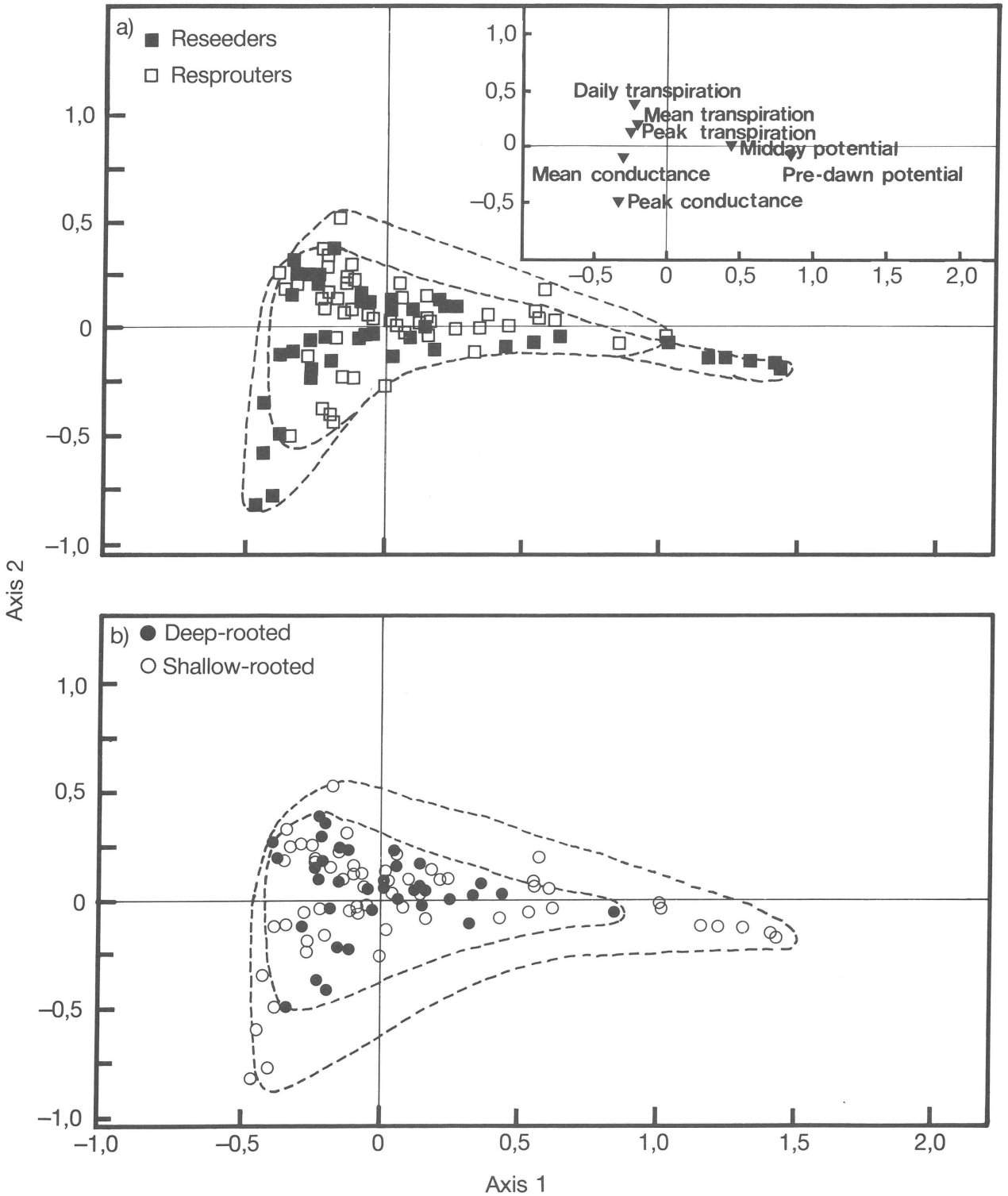

Figure 6 The separation of: (a) reseeders and resprouters; and (b) deep-rooted and shallow-rooted plants according to their physiological responses to environmental conditions after fire at Swartboskloof. Axis 1 and 2 account for 63% and 23% respectively of the inertia in the ordination by correspondence analysis. Each symbol summarizes the physiological response of one taxon on one day. The positions of the physiological response factors in the ordination space are shown in the insert. The relative contribution (%) of the factors to the total inertia for axes 1 and 2 are: predawn xylem pressure potentials (16; 0); midday xylem pressure potentials (57; 1); mean stomatal conductance (6; 4); peak stomatal conductance (9; 54); mean transpiration rate (4; 6); peak transpiration rate (4; 4) and daily water use per unit leaf area (4; 31).

first winter rains after the summer drought. These first rains may not have wet the soil to any great depth as the upper soil layers were so dry at this stage that most water was probably absorbed by this layer. Most of the resprouters probably have access to soil moisture throughout the season (due to their deep root systems) and therefore do not show as marked a response. Similar patterns are evident in the chaparral. For example, the shallow-rooted *Arctostaphylous stanfordiana* displays higher transpiration rates than deep-rooted *Adenostoma fasciculatum* for most of the year. Both species, similar to the plants of our study, showed a decline in transpiration during the summer drought, although the response was more moderate for *A. fasciculatum* (Hart & Radosevich 1987).

The slightly higher peak conductances and transpiration rates and lower water potentials of the shallow-rooted species when compared to the deeper-rooted species of our study, suggest that they tend to extract water quite rapidly whenever it is available. The deeper-rooted resprouters tend to be more moderate water users, seldom showing high conductances or transpiration rates and maintaining low xylem pressure potentials throughout the year. These findings provide support for Cohen's (1970) theory that shallow-rooted, drought-adapted plants with overlapping root systems extract water rapidly while it is available whereas deeper-rooted plants with non-overlapping roots are more conservative in their soil water utilization.

In the correspondence analysis the most pronounced segregation of species/regeneration types in the ordination reflects the summer drought experienced by the shallow-rooted plants. This effect is clearly illustrated by comparing seedlings and resprouts of *P. nitida* (Figure 7). This illustrates that differences between taxa are due to rooting depth rather than regeneration mode.

Canopies (leaf area and biomass) of reseeding plants take considerably longer to recover after fires than those of resprouters. Due to the high percentage of resprouting species in Swartboskloof (65%; G.G. Forsyth, unpublished data) post-fire biomass recovery was rapid. Our results showed that transpiration rates per unit leaf area of reseeders and resprouters *per se* were not significantly different, validating the assumption made in Bosch *et al.*'s (1986) model. The time taken for post-fire water yields to return to prefire levels would therefore depend primarily on the vegetation recovery rate (governed by the seeder:sprouter ratio), with water use per unit leaf area being similar.

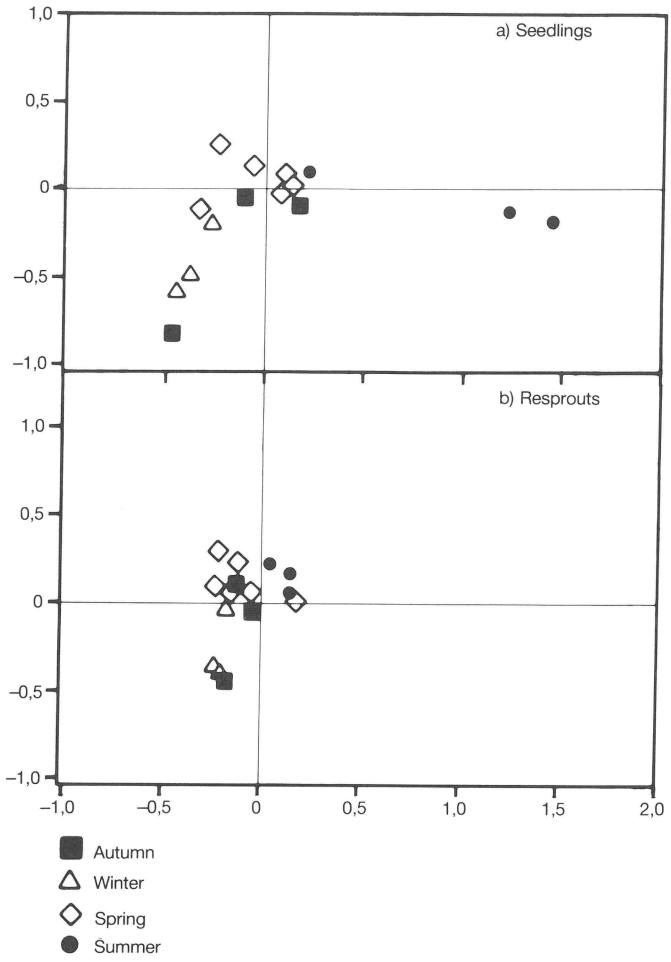

Figure 7 The seasonal separation of *Protea nitida* (a) seedlings and (b) resprouts according to their physiological responses to environmental conditions after fire at Swartboskloof. Ordination particulars as for Figure 6.

Conclusions

Reseeders and resprouters do not differ markedly in their water use per unit leaf area except during the dry season and the period immediately thereafter where differences appear to be related to root depth (rather than regeneration form). Differences were evident therefore, between shallow- and deep-rooted species, with shallow-rooted species displaying generally higher transpiration rates throughout the year than deep-rooted species, and experiencing lower water potentials during periods of low soil water. Our results suggest that, for the purpose of predicting water use, fynbos plants should be grouped according to functional attributes such as rooting behaviour rather than regeneration mode. We conclude that leaf area development can be used as a simple predictor of post-fire catchment water yield changes.

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